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# Aggregation in a Tropical Neritid

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*Abstract.* Aggregation by the tropical intertidal mollusk *Nerita scabricosta* was examined. This behavior reduced mortality rates, especially for smaller snails. Habitat selection, size-specific differences in movement patterns, and the physical structure of the substratum were important in the formation and maintenance of aggregations.

## INTRODUCTION

SNAILS of the genus *Nerita* (Archaeogastropoda) are common inhabitants of tropical hard-substratum shores. *Nerita scabricosta* (Lamarck, 1822) inhabits the upper levels of exposed rocky shores (GALTSOFF, 1950; HEDGPETH, 1969) from Baja California to Ecuador (KEEN, 1971).

In Panama, *Nerita scabricosta* (hereafter referred to as *Nerita*) exists in a harsh environment (GARRITY, 1984). Many shorelines throughout the world are covered by macroalgae and/or sessile invertebrates (LEWIS, 1964; STEPHENSON & STEPHENSON, 1972); these ameliorate physical conditions during low tides by shading the rock and/or retaining water, and can provide shelter to other organisms. The Pacific coast of Panama is barren of macroalgae (EARLE, 1972), and dense beds of mussels, barnacles, or oysters are rare (GARRITY & LEVINGS, 1981; MENGE & LUBCHENCO, 1981). Low tide temperatures on this tropical shore can exceed 50°C (GARRITY, 1984). Further, *Nerita* is more-or-less constantly exposed to terrestrial conditions—snails move downshore behind falling tides from resting positions above the high water mark, then move upshore ahead of rising tides (GARRITY & LEVINGS, 1981).

Some mechanisms mollusks use to lessen physical stress on this region's rocky shores have been examined (GARRITY, 1984). *Nerita scabricosta* avoids potentially lethal daytime conditions by (1) a limited, cyclic activity period, (2) the selective use of microhabitat, and (3) evaporative cooling. Here we examine the occurrence, function, and formation of multilayered aggregations in *Nerita,* and show that this behavior enhances individual survival. Differential movement patterns among size classes and the structure of the preferred microhabitat result in a typical size layering within aggregations, with smaller, more vulnerable individuals located beneath larger snails.

## METHODS

### Occurrence and Numerical Composition of Aggregations

We sampled four sites along the Pacific coast of Panama (Uva, Chitre, Taboguilla, and Naos Islands) during the period October 1982 to April 1983. We chose sunny days, when snails were inactive. At each site, we laid a 100-m transect tape along the shore in the splash zone. We then walked along the tape. As snails were encountered, we recorded whether they were solitary or aggregated (in contact with conspecifics), and counted the number of snails in each aggregation. We recorded whether snails were in "exposed" (defined as sloping, horizontal, or vertical rock) or "protected" (defined as crevices and tidepools) microhabitats. Protected microhabitats remain cooler and/or wetter during daytime exposures (GARRITY, 1984, fig. 2, table 2). Because *Nerita* strongly prefers crevices and tidepools (GARRITY, 1984), this method undersampled aggregations in exposed microhabitats. Transect lines were extended laterally and additional data taken in

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exposed microhabitats until sample sizes were equal to those from protected microhabitats.

### Three-dimensional Size Structure

We examined the three-dimensional structure of four aggregations of varying size on Culebra, Naos, and Uva Islands during sunny days in 1979 and 1983. We dissected aggregations layer by layer, marking the dorsal surfaces of all visible snails with chalk, removing them, and then repeating this on each successive layer until all were collected. We measured the shell lengths of snails in each layer with Vernier calipers.

### Water Holding Capacity

*Nerita scabricosta* holds water extraviscerally in its nonpartitioned shell (Vermeij, 1978). Individuals lose water during the day; this evaporation cools tissues significantly (Garrity, 1984). We tested the relationship between snail size and the amount of free water held by removing inactive individuals of various sizes from the rock on Naos Island on an early morning, falling tide and quickly placing each over a funnel inserted into a small, preweighed vial. Snails expelled water into the vials as they withdrew into their shells. The water in each vial was weighed and plotted against shell length.

### Effects of the Number of Snails in an Aggregation

To test the hypothesis that stress decreases with increasing numbers of individuals per aggregation, we set out groups of 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 75, 100, 125, 150, 175, 200, and 300 freshly collected *Nerita* on a sloping surface on Uva Island (30 March 1983). Each group contained small, medium, and large individuals. Seawater was poured over each at the start of the experiment. This gave all snails access to extravisceral water, and wetted the rock so all snails could move freely within each group. After 6 h (0900–1500) groups of snails were collected and placed in separate mesh containers in a 50-L cooler filled with seawater aboard the R/V *Benjamin*. Water was changed at frequent intervals. After 24 h we examined each group and counted surviving snails.

### Effects of Snail Size

To test the effect of size on susceptibility to physical stress, we collected ~600 specimens of *Nerita* from Naos Island and divided them into three groups: small (2–6 mm shell length), medium (12–16 mm) and large (22–26 mm). We kept snails overnight in shaded, running seawater tanks at the Naos Marine Laboratory, and then for the next three days (7–9 March 1983) placed subsamples of each group, in spaced arrays, on flat rock in the high zone of Naos Island. To prevent movement out of the spaced arrays, snails were not watered initially (as above). After 6 h we collected them and placed each group in laboratory tanks. We counted the number of survivors after 24 h.

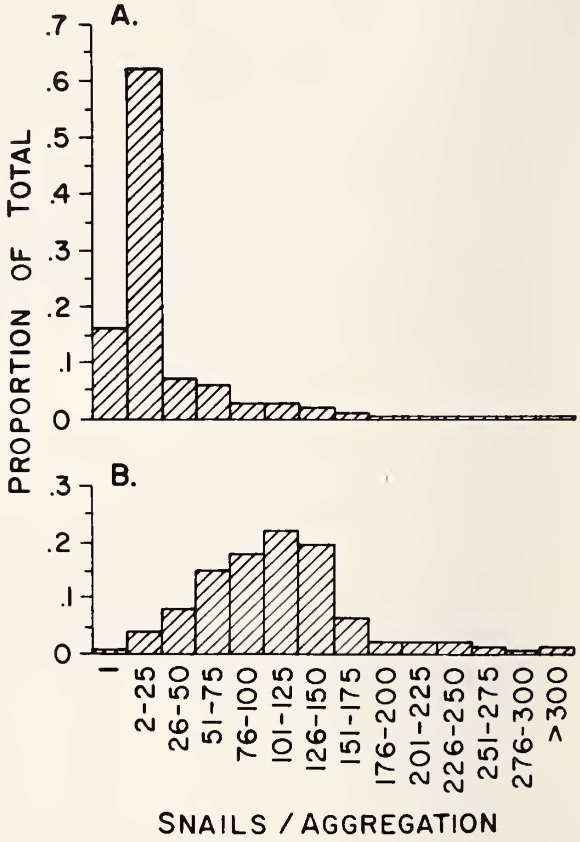

Figure 1

Distributions of aggregation sizes of *Nerita scabricosta*. Data are the proportions of different size classes of aggregations encountered in 800 aggregations sampled in (A) protected and 800 in (B) exposed microhabitats within a given range of number of snails. See text for further information.

### Formation of Aggregations

We observed the behavior of 50 previously marked (but otherwise undisturbed) small, medium, and large (see above section) snails in the field as they (1) became active on falling tides and left aggregations to graze, (2) foraged over wet or damp rock, and (3) became inactive either as the rock dried or as high tide approached. We recorded the number of snails that were active and the duration of activity, and looked for evidence of homing or trail-following behavior.

The role of substratum heterogeneity in the formation of aggregations was examined in April 1983 on Naos Island. We used four groups of ~200 snails (each group encompassing the natural size range of *Nerita*). Snails from each group were placed, as closely spaced but solitary individuals, on (1) a flat surface (exposed microhabitat), (2) a flat surface with several shallow depressions (semi-exposed), (3) a flat surface adjacent to a crevice (protected), and (4) a flat rock adjacent to a vertical surface (semi-protected). They were set out at the approximate high tide mark, on a rising tide just prior to the normal onset of activity, and examined for evidence of aggregation after 2 h (high tide), when movement had ceased.

## RESULTS

We pooled data on the distribution of numbers of snails in aggregations of *Nerita,* because they did not differ among sites (Chi-square tests, $P > 0.1$). However, differences in the distribution of aggregation size classes between "exposed" and "protected" microhabitats were striking (Figure 1, Chi-square test, $P < 0.001$). Aggregations in crevices and tidepools had significantly fewer individuals (median number = 24) than those on vertical or flat rock (median number = 109, Mann-Whitney U test, $P < 0.001$). Snails aggregated in every microhabitat, but fewer than 1% occurred as solitary individuals (n = 4) on open surfaces compared to 16% (n = 124) in crevices and tidepools. It should be again noted that we did not sample all microhabitats with equal effort and are here comparing only the distribution of sizes of aggregations between exposed and protected microhabitats.

Dissections of aggregations in the field showed differences in snail size among layers (Figure 2). Larger individuals occurred primarily in the outer layers, and increasingly smaller snails formed the inner layers. This occurred over a range (59–209 snails) of aggregation sizes (Figure 2).

The amount of water held extraviscerally was positively related to snail shell length (Figure 3). These data best fit an exponential curve ($y = 0.01e^{0.18x}$, $r^2 = 0.90$, $n = 40$), indicating large snails hold proportionately more water than small ones (as expected from geometric considerations).

Both aggregation size and the size of individual snails were important in reducing physical stress. First, when groups containing different numbers of snails were set out on Uva Island for 6 h, there was a rough inverse relationship between mortality and aggregation size (Table 1, Spearman rank correlation coefficient = −0.97, $P < 0.01$). Mortality was highest (>80%) among snails in aggregations of ≤25 individuals. Mortality ranged from 17–73%

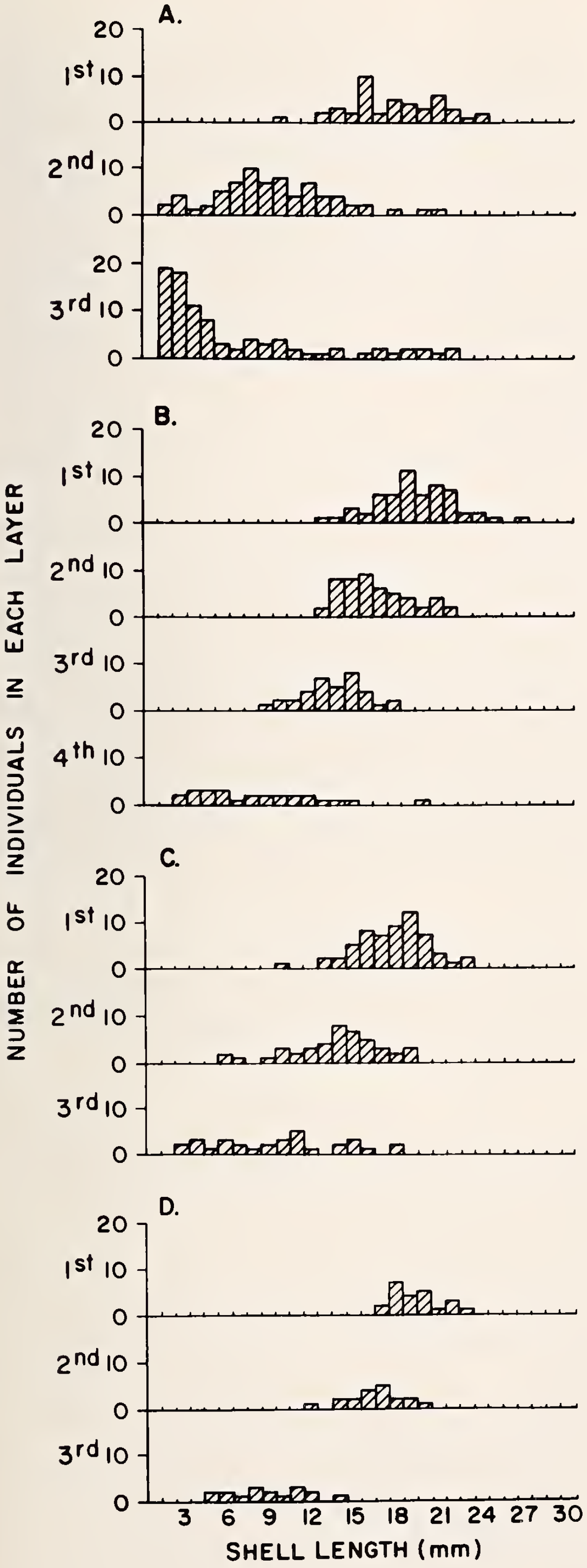

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Figure 2

Sizes of *Nerita scabricosta* in the layers of aggregations. Data are the number of snails of a given size (shell length in mm) in each layer from four different aggregations. A. Aggregation on a vertical surface, n = 209, Uva. B. Aggregation from a crevice, n = 170, Culebra. C. Aggregation on a vertical surface, n = 134, Culebra. D. Aggregation from a small crevice, n = 59, Naos.

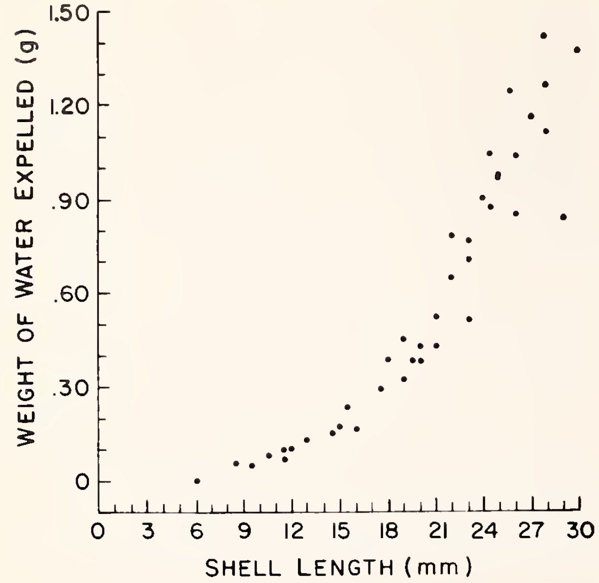

Figure 3

Amount of water held within the shell *vs.* shell length. Regression equation is: $y = 0.01e^{0.18x}$, $r^2 = 0.90$. See text for further explanation.

in aggregations of up to 100 snails. Only groups of 125 or more experienced less than 10% mortality, and there were two deaths in the largest (n = 300) group. Second, snails set out as solitary individuals on Naos Island showed size-dependent differences in mortality rates (Table 2).

Table 1

Mortality of *Nerita scabricosta* in artificially constructed clumps. Clumps were constructed on Uva Island and set out for 6 h during low tide. Snails were placed in mesh containers in frequently-changed seawater and survivors counted after 24 h.

| Aggregation size | Number dead | Percent mortality after 24 h |
|---|---|---|
| 5 | 4 | 80 |
| 10 | 9 | 90 |
| 15 | 13 | 87 |
| 20 | 17 | 85 |
| 25 | 21 | 84 |
| 30 | 22 | 73 |
| 35 | 19 | 54 |
| 40 | 18 | 45 |
| 45 | 20 | 44 |
| 50 | 23 | 46 |
| 75 | 22 | 29 |
| 100 | 17 | 17 |
| 125 | 8 | 6 |
| 150 | 6 | 4 |
| 175 | 3 | 2 |
| 200 | 4 | 2 |
| 300 | 2 | 1 |

Table 2

Mortality of spaced *Nerita scabricosta*. Snails were placed in spaced arrays on flat rocks for 6 h during low tide. They were then placed in running, shaded seawater and survivors counted after 24 h.

| | Large (22–26 mm) | | Medium (12–16 mm) | | Small (2–6 mm) | |
|---|---|---|---|---|---|---|
| | N tested | N died | N tested | N died | N tested | N died |
| Day 1 | 46 | 4 | 51 | 34 | 55 | 51 |
| Day 2 | 75 | 5 | 75 | 29 | 75 | 58 |
| Day 3 | 75 | 7 | 75 | 51 | 75 | 70 |
| Total | 196 | 16 | 201 | 114 | 205 | 183 |
| Proportion dead | .08 | | | .57 | | .89 |

Snails died in all size classes, but significantly fewer large snails died than medium ones (8% *vs.* 57% overall, Chi-square test, $P < 0.001$), and significantly fewer medium-sized snails died than small *Nerita* (57% *vs.* 89% overall, Chi-square test, $P < 0.001$). Some mortality in these experiments may have resulted from handling; however, all snails were handled in the same way. High rates of mortality do not reflect events in nature. Snails were set out in flat or sloping homogeneous rock (very exposed microhabitat) to facilitate comparisons among treatments.

Observations of marked individuals in the field showed shell size was an important variable in patterns of movement (Table 3). During the tidal cycle, more large snails

Table 3

Movement patterns for differently-sized *Nerita scabricosta*.

A. Percent movement.[1]

| | Time | | | | | | |
|---|---|---|---|---|---|---|---|
| Snail size | High tide | +2 h | +4 h | Low tide | +8 h | +10 h | High tide |
| Small | 0 | 11 | 0 | 0 | 0 | 8 | 0 |
| Medium | 0 | 47 | 12 | 3 | 1 | 16 | 0 |
| Large | 0 | 64 | 35 | 9 | 14 | 51 | 1 |

B. Distance moved.[2]

| Snail size | Median | Range | Probability |
|---|---|---|---|
| Small | 0.1 m | 0.03–0.48 | <0.001 |
| Medium | 1.3 m | 0.06–4.14 | <0.001 |
| Large | 3.62 m | 0.05–6.70 | |

[1] Percent of 50 snails in each size class active at a given time over a complete tidal cycle (12 h). Small snails = 2–6 mm, medium snails = 12–16 mm, large snails = 22–26 mm.

[2] Distance moved from resting position, measured as outward path for the same snails as in (A); size classes as in (A). Probabilities are from comparisons of the distance moved by small and medium, and medium and large snails, using Mann-Whitney U tests.

became active than medium snails (Sign test, $P = 0.031$) and more medium snails were active than small ones ($P = 0.016$). A similar gradient appeared in the distances that differently sized, active individuals moved (Table 3B); the median distance moved by large snails (3.6 m) was significantly greater than that by medium snails (1.3 m), and the latter was significantly greater than for small snails (0.1 m, Mann-Whitney U tests, $P < 0.001$, both cases).

Snails of all sizes moved as the tide fell, but small snails were active for <0.5 h and moved back into crevices and aggregations as the rock dried. Seventeen of 50 medium and 38 of 50 large individuals moved downshore with the tide, rather than moving back. Larger snails sometimes followed visible trails left by conspecifics when moving up or downshore ($n = 23/108$), but seldom did so when grazing at lower levels ($n = 5/87$). Individuals did not always move back to the same aggregation or position. Over a five-day period, 33 of 50 large, marked snails dispersed to several other aggregations within 5 m of the original one. Net lateral movement along the shore is usually slow, except in the presence of the predaceous gastropod *Purpura pansa* (Garrity & Levings, 1981).

The nature of the substratum plays a role in the formation and structure of aggregations. Of the specimens of *Nerita* ($n = 200$) placed upon a flat, homogeneous surface, 127 remained solitary, and all aggregations had a single layer. The second group of 200 clustered around depressions present on the rock; again there were no multilayered groups and 58 snails remained solitary. Snails placed adjacent to a crevice all ($n = 201$) moved into it. Within the crevice, 26 were solitary and the rest in multilayered aggregations. Finally, *Nerita* placed adjacent to a vertical surface moved either to the angle formed by the intersection of the two surfaces where they formed a large ($n = 185$), multilayered aggregation, or onto the vertical surface ($n = 12$ aggregated in a single layer, 3 solitary).

## DISCUSSION

Aggregation in limpets (review in Branch, 1981) and other herbivorous gastropods (Rohde & Sandland, 1975; Vannini & Chelazzi, 1978, and included references) has been related to abiotic factors such as desiccation, wave action, or insolation, although the causes of this behavior have not been shown. Considerable evidence supports the notion that aggregation is an important mechanism to reduce physical stress in *Nerita scabricosta*. First, in natural situations, both the occurrence of snails in aggregations and the number of individuals per group were greatest in harsher microhabitats (Figure 1). Even in more benign microhabitats, the majority (84%) aggregated. Mean tissue temperatures of snails in aggregations stay significantly lower than those of solitary ones throughout the day, both on open rock and in crevices (Garrity, 1984, fig. 11), and the mortality rate of aggregated snails is lower than that of solitary ones (Garrity, 1984, table 5). Field manipulations of aggregation size in an exposed microhabitat showed members of larger groups survived better than *Nerita* in small ones (Table 1).

Most aggregations consisted of two or more layers and had a distinct size structure; larger individuals occurred chiefly in the top layer and the proportion of smaller snails increased with depth (Figure 2). The smallest size classes were never represented in the top layer. This size structure may have chiefly benefited small *Nerita,* because they held proportionately less water (Figure 3) and were most vulnerable to stress (Table 2). Snails in the interior of aggregations were both shaded and dampened by those above; it also is likely, given the movement pattern of small *Nerita* (Table 3B), that water trickled by larger snails in aggregations was a source of extravisceral water for small ones in bottom layers. Although water lost by solitary snails decreases with size, larger individuals in aggregations lose proportionately more water than small ones (Garrity, 1984, fig. 12).

The formation and maintenance of aggregations had several components. Perhaps most importantly, *Nerita* chose crevices and tidepools, comprising <20% of the rock surface in the splash zone (Garrity, 1984, fig. 1), and avoided more exposed areas of the rock during periods of inactivity (Levings & Garrity, 1983, table 3). This behavior gave inactive *Nerita* a clumped distribution in space. Second, size-specific activity patterns tended to maintain aggregations and could result in snails being layered by size: small individuals moved short distances and were active only briefly before returning to aggregation sites (Table 3). As shell size increased, so did foraging time and distance (Table 3; also see Levings & Garrity, 1983, fig. 2). Larger snails moved into aggregations last, and thus occurred in the outer layers. The nature of the substratum may enhance this effect. Crevices, the most preferred microhabitat, are wider at the mouth than at the bottom. Larger snails were thus excluded from bottom layers (see also Raffaelli & Hughes, 1978). Small crevices, pocks, or depressions are probably foci for aggregations found on horizontal or sloping surfaces. The occurrence of these microsites in nature was not monitored in our transects. However, when groups of 200 spaced snails were placed (a) on flat, homogeneous rock and (b) on a flat surface containing several small depressions, more of the second group aggregated, and aggregations centered on the depressions. Lastly, larger *Nerita* moved up- and downshore as a wave front immediately behind falling tides and ahead of rising tides (Garrity & Levings, 1981). During this vertical movement, individuals frequently followed slime trails of leading snails. These two behaviors resulted in a clumped distribution when *Nerita* moved to or from refugia.

*Nerita scabricosta* actively avoids submergence. This reduces exposure to predaceous fishes (Bertness *et al.*, 1981), but results in increased exposure to potentially lethal conditions during the day. Behavioral mechanisms used by *Nerita* to reduce desiccation and thermal stress include a reduced activity period, microhabitat selection, and evaporative cooling. These mechanisms are enhanced by the formation of multilayered aggregations of up to several hundred snails, resulting from size-specific differences in behavior and activity patterns, and by the physical structure of preferred microhabitats. Aggregation is an important mechanism, especially for smaller *Nerita,* for the reduction of stress on this harsh tropical shore.

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